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A FOSSIL FAUNA OF EARLY TERRESTRIAL ARTHROPODS FROM THE GIVETIAN (UPPER MIDDLE DEVONIAN) OF GILBOA, NEW YORK, USA

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INTRODUCTION

A series of remarkably preserved fossils of early land arthropods was discovered in 1971 in the course of digesting rock specimens from Gilboa, New York, in hydrofluoric acid (HF) for plant fossils. The material occurs in a dark gray shale making up part of the Panther Mountain Formation, and is of Middle Givetian age (376-379 million years old). The initial announcement and preliminary description of the find (SHEAR *et al*, 1984) indicated that among the most common remains were those of the extinct arachnid order Trigonotarbida, also reported from the two other sites where terrestrial animals of Devonian age have been found.

The Gilboa fossils are younger than those from the other two sites. Alken an der Mosel, Germany, has been dated as Lower Emsian (STØRMER, 1976), and Rhynie, Scotland, as Siegenian (ROLFE, 1980). While the preservation of the Rhynie material is excellent, the specimens are embedded three-dimensionally in a glassy chert and appear to consist of fragile, fragmentary carbon films; I doubt that they could be removed from the matrix. Thus study of these fossils is limited to what is visible in the sherds of chert and to the orientations already available. At Alken, the fossils are preserved conventionally in a shale, with some of the carbonized cuticle adhering.

The unique aspect of the Gilboa fossils is that while they have evidently been carbonized and subjected to heat and great pressure, even the finest details of cuticular structure (setae, trichobothria, slit sense organs) remain. These fossils can be extracted from the matrix and mounted on microscope slides for detailed study. A modest number of more or less complete specimens have been found and these guide the reconstruction process based on the more numerous identifiable fragments.

The trigonotarbids, collembolans, mites, and possible spiders from Rhynie (HIRST, 1922) have the distinction of being among the oldest known fossils of definitely terrestrial animals (the *very* oldest are millipeds from the Upper Silurian of Britain [ALMOND, 1985]), but they already show such a high level of adaptation to the terrestrial habitat that we are forced to conclude that invasion of the land by these and other arthropod groups took place much earlier than the Siegenian.

OCCURRENCE AND PRESERVATION

All material was obtained from plant fossiliferous slabs of gray shale in the upper part of the Panther Mountain Formation, from the west flank of Brown Mountain, Gilboa, New York (see BANKS et al., 1972, for details). The Panther Mountain

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Formation belongs to the Tioughniogan Stage of the Erian Series, which is the approximate equivalent of the Middle Givetian of Europe.

To date (end of 1985), more than 1500 microscope slides of arthropod fragments have been prepared. These contains 5000 or more fragments. Most of the fragments are less than 1 mm in their largest dimension. About 20% of the fragments can be identified. A majority of the cuticular scraps is featureless and therefore unidentifiable.

Most of the Gilboa fossils, as they appear in the slide preparations, are discrete body parts, e. g., leg podomeres, tergites, and cuticle scraps. Only very rarely are complete, more or less articulated individuals found. At this time, only twelve such specimens have been collected (four trigonotarbids, two centipeds, seven mites, and a single pseudoscorpion) out of a total of about 5000 fragments. This raises the question of whether potential whole animal fossils are being dissociated during preparation, for example when the rock is broken up before acid digestion. I do not believe this to be the case, since digestion of bulk, unbroken subsamples produced material that is qualitatively the same as that obtained from fragmented samples.

Early in the course of this work, our research team (myself, P.M. Bonamo, J.D. Grierson, and W.D.I. Rolfe) gave consideration to the possibility of contamination by arthropod debris during collection or preparation. This was ruled out because (1) the palaeobotanical laboratory at Binghamton, New York, where the fossils are prepared, is designed to exclude such contamination at the level of pollen and spores, (2) the specimens are thoroughly washed before digestion, (3) many of the taxa present have been extinct for hundreds of million of years or represent forms not found in the Gilboa region or even North America, and (4) the observation of one specimen with its limbs still embedded in the unaltered rock. The point which assures the genuiness of these fossils is their highly flattened state, and characteristic appearance in incident light: opaque, somewhat silvery, and dully reflective. Living material treated in the same way (HF digestion, etc.) is not flattened and becomes so transparent that it virtually disappears under incident light. The rare occurence of a contaminant (two small fly larvae, several pollen grains, and a plant fragment have been found on a few of nearly 1500 slides; one of these slides was not made in the Binghamton laboratory) is therefore easily detected. While skepticism may still be expressed about the provenance of the Gilboa animals, we see no further ways to demonstrate their authenticity and consider the case on recent contamination to be closed.

The remarkable preservation of these specimens is revealed only when they are examined with a microscope under transmitted light. They then appear as translucent, yellowish brown to dark reddish brown films, reminiscent of sclerotized arthropod cuticles. In incident light, the fossils appear as tiny, matt brown to silvery black flakes with an irregular, dully reflective surface. They would be unrecognizable on the surface of the gray shale in which they are found; repeated examination of rock chips later confirmed as containing fossils has borne this out.

The effects of compression are obvious and account for the lack of detail seen in incident light. Setae and other relief were pressed into the plane of the fossils, and are revealed only through the use of transmitted light or scanning electron microscopy. Heat, pressure, and time may have resulted in the reduction of much of the organic matter in the fossils to carbon, though this is conjectural –none of the material has been analyzed for residual organic molecules.

Replacement seems not to have occured to any significant degree. GRIERSON (1976) has described pyrite replacement from the plants collected with the animal fossils. I have seen small, rectangular crystals on the surface as well as inside of some of the fossils, but suspect that pyrite replacement to any degree would lead to opacity, which is not observed.

The quality of preservation is best illustrated by the accompanying photographs, and includes the preservation of setae, trichobothria (extremely delicate sensory setae), slit

sense organs and lyriform organs, and cuticular microsculpture. Setae are often found still in place in their sockets, or even lying beside their sockets, presumably having been broken off during the flattening of the fossil. It is worth noting that in alcohol-preserved specimens of extant spiders trichobothria and setae are often missing, broken off by handling or by agitation of the preservative. Because of the fragmentary nature of these fossils and the flattering to which they have been subjected, the preservation of detail in the Gilboa material is in some ways inferior to that of the Rhynie trigonotarbids. However, those specimens cannot be removed from the matrix and can only be studied in detail if they happen to be near the surface of the sherd in which they are found; the chipping and grinding technique may partially destroy many specimens. The present fossils complement the Rhynie material by permitting the study of cuticular detail that is difficult to resolve in the Rhynie fossils.

TECHNIQUES OF STUDY

The specimens have been studied using a variety of microscopic techniques. Under a binocular dissecting microscope, both incident and transmitted light can be used by varying the position of a white card beneath the specimen, and varying the angles at which light from fiber optic guides strikes the specimen. Using fiber optics for surface illumination and a built-in light source for transmitted light, both rheostatically controlled, a wide variety of conditions of lighting at all magnifications save 1000x was obtained under the compound microscope. I found Nomarski Interference Contrast optics particularly useful for the clarification of small details, and using the optical sectioning properties of this technique, I was able to separate the closely appressed upper and lower surfaces of the fossils. Scanning electron microscopy proved less useful than I originally thought, because details visible in transmitted light do not come through unless they are directly on the surface examined.

The fossil arthropods from Gilboa will be deposited in the Department of Invertebrate Paleontology of the American Museum of Natural History, New York. A selection of specimens will also be placed in the British Museum (Natural History).

TAPHONOMY

I suspect that many of the fossils represent exuvii. This is shown by shrivelling of some specimens, the thin nature of some of the cuticles, and by the occurrence of isolated body regions such as several trigonotarbid carapaces– structures which modern spiders and amblypygids detatch along the margin during molting so that they often become dissociated from the rest of the exuvium. Overfolded regions of cuticle may be separated from the main area of cuticle by some distance, and presumably these were separated by sediment before acid dissolution. No such spaces indicating the former presence of sediment are found occupying body cavities of the arthropods. They must therefore either have been flat on arrival at their burial site, perhaps due to dessication elsewhere, or have been flattened immediately thereafter, before sediment could wash into such lacunae.

The arthropod fragments may occasionally have parts displaced relative to one another and be folded, presumably as a result of compression of flexible cuticles which arrived in a contorted state at the site of deposition.

Rarely, fragments may show a degree of contortion too excesive to explain by the simple accumulation of folded fragments to form a felted mat. W.D.I. ROLFE has suggested that some of these are rejectamenta–husks of arthropod prey discarded after crushing and external digestion of soft tissues by arachnid predators. Such rejectamenta are today characteristic of arachnids with toothed chelicerae. Some may be rejectamenta produced by trigonotarbids themselves. This topic will be reviewed towards the end of

the Gilboa project, when the question of the levels of the ecological pyramid represented by the fossils will be considered.

Some explanation is required for the minute size of the fossils recovered and for the absence of larger arthropods, or larger fragments of them. We think it significant that the rocks most productive of animal fossils are those containing almost soild mats of interlacing *Leclerqia* (Lycopsida) stems (BANKS et al., 1972); SHEAR et al. (1984) have suggested that the small animal fossils occur as particles retained within a three-dimensional sieve formed by the spinose leaves on a meshwork of such *Leclercqia* stems. Larger fragments would have been excluded by such a sieve, while finer bits of animal material passed through. Our specimens therefore seem to sample a range of sizes small enough to be transported by the current but large enough to be retained by the *Leclerqia* filter.

The fine grain size of the containing shale indicates settlement from sluggishly moving waters, which may have carried arthropod fragments into the sieve from some distance away.

PALEOECOLOGY

Almost all the arthropods recovered were terrestrial forms which may have lived among or on the *Leclercqia* stems themselves. The only exception to this is the presence of eurypterid fragments. These may have been amphibious forms, or aquatic forms introduced by the flooding that invaded the plant stands.

Such a scenario confirms that suggested by BANKS et al. (1985) for the exceptional preservation of the Gilboa plants: "These plants were not transported prior to fossilization. They must have lived close to areas of quiet water either in swamps or pond edges, or possibly along the leeves of streams. In any case, to be so well preserved, they had to have been buried in situ."

ELEMENTS OF THE FAUNA

A detailed series of papers on the individual arthropod groups found among the Gilboa fossils will be published in succeeding years. Here, I briefly characterize the material recovered so far.

As at Rhynie, the fauna appears to be dominated by members of the extinct Order Trigonotarbida (Arachnida). At least five clearly distinct species occur; it is fairly certain these different forms do not represent developmental stages of fewer species. The largest entire specimen yet recovered is about 2 mm long. Isolated podomores, tergites and chelicerae suggest, however, that the largest specimens may have been more than 10 mm long (SHEAR, SELDEN, ROLFE, BONAMO and GRIERSON, in prep.). ROLFE (1980) correctly disregarded the suggestion of KEVAN et al. (1975) that the Rhynie trigonotarbids were spore feeders; the adaptations of these animals and of the closely related Gilboa forms are clearly those of predators.

Two species of mites have been found, and are represented by the most exquisitely preserved specimens in the collection. One species belongs to the living family Ctenacaridae and is the oldest known oribatid mite; the other is still under study (NORTON, SHEAR, BONAMO and GRIERSON, in prep.). However, both mite species show adaptations suggestive of feeding on organic debris or fungi, as do modern ctenacarids.

Evidence suggesting the presence of spiders and scorpions is equivocal. Some podomeres and a fragmentary chelicera closely resemble those of araneomorph spiders, and a single leg tarsus appears to be scorpionoid.

Four specimens of a pseudoscorpion have been recovered. This record represents the only Paleozoic occurrence known for the group, and pushes back the earliest date for them by a factor of 10. The material has not been studied in detail, but the chelicerae appear to have all of the characteristic modifications of modern pseudoscorpions,

including a galea, flagellum, and internal and external serrulae. All modern pseudoscorpions are predatory.

Scraps of eurypterid cuticle, with its characteristic nodular scales, are fairly common, as are tarsi from the grasping appendage of a eurypterid (at first erroneously attributed to amblypygids).

Among the best preserved specimens are those of a centiped which was first thought to be close to the enigmatic craterostigmatomorphs. Since that suggestion was made, even better material has been found which now seems to ally the fossil species to the Lithobiomorpha, perhaps the subfamily Anopsobiinae. Pieces of podomeres and antennae hint at the presence of a scutigeromorph centiped as well. All known living centipeds are predators.

Another myriapod group recently identified among the Gilboa fossils is the extinct Class Arthropleurida. Carboniferous arthropleurids were as large as 2 meters in length; the Gilboa species was probably less than 5 mm long. For the first time, complete heads of arthropleurids have been found and study of them will do much to settle the relationships of this unsual group.

Fragmentary compound eyes and cuticular scraps may be from machilid insects. If so, these are the oldest insect fossils in the world.

I expect that further arthropod groups will appear among the fossils. Of the several tons of material collected from the now-submerged collecting site, less than 20 kg have been processed, most of this from three subsamples. Gilboa will prove to be the clearest "window" yet opened on the terrestrial ecosystems of the Devonian Period.

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SUMMARY

A remarkably well preserved fauna of terrestrial arthropods was discovered in 1971 in Givetian (Devonian) shale near Gilboa, New York. The fossils can be removed from their matrix and mounted on microscope slides for study by transmitted light. The fauna is by far the most diverse yet discovered for Devonian terrestrial arthropods and includes trigonotarbid arachnids, pseudoscorpions, centipeds, mites, and eurypterids. Spiders, scorpions, and insects may also be present. As with the other two known Devonian terrestrial arthropod faunas, the Gilboa fauna is dominated by predatory arachnids.